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Susceptibility of ponderosa pine, *Pinus ponderosa* (Dougl. ex Laws.), to mountain pine beetle, *Dendroctonus ponderosae* Hopkins, attack in uneven-aged stands in the Black Hills of South Dakota and Wyoming USA

José F. Negrón [a,*], Kurt Allen [b], Blaine Cook [c], John R. Withrow Jr. [d]

[a] *USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect, Fort Collins, CO 80525, United States*
[b] *USDA Forest Service, Forest Health Management, Rapid City Service Center, 8221 S. Highway 16, Rapid City, SD 57702, United States*
[c] *USDA Forest Service, Black Hills National Forest, 8221 S. Highway 16, Rapid City, SD 57702, United States*
[d] *SI International, Rocky Mountain Research Station, USDA Forest Service, 240 West Prospect Road, Fort Collins, CO 80525, United States*

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Abstract

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins can cause extensive tree mortality in ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., forests in the Black Hills of South Dakota and Wyoming. Most studies that have examined stand susceptibility to mountain pine beetle have been conducted in even-aged stands. Land managers increasingly practice uneven-aged management. We established 84 clusters of four plots, one where bark beetle-caused mortality was present and three uninfested plots. For all plot trees we recorded species, tree diameter, and crown position and for ponderosa pine whether they were killed or infested by mountain pine beetle. Elevation, slope, and aspect were also recorded. We used classification trees to model the likelihood of bark beetle attack based on plot and site variables. The probability of individual tree attack within the infested plots was estimated using logistic regression. Basal area of ponderosa pine in trees $\geq$25.4 cm in diameter at breast height (dbh) and ponderosa pine stand density index were correlated with mountain pine beetle attack. Regression trees and linear regression indicated that the amount of observed tree mortality was associated with initial ponderosa pine basal area and ponderosa pine stand density index. Infested stands had higher total and ponderosa pine basal area, total and ponderosa pine stand density index, and ponderosa pine basal area in trees $\geq$25.4 cm dbh. The probability of individual tree attack within infested plots was positively correlated with tree diameter with ponderosa pine stand density index modifying the relationship. A tree of a given size was more likely to be attacked in a denser stand. We conclude that stands with higher ponderosa pine basal area in trees $>$25.4 cm and ponderosa pine stand density index are correlated with an increased likelihood of mountain pine beetle bark beetle attack. Information form this study will help forest managers in the identification of uneven-aged stands with a higher likelihood of bark beetle attack and expected levels of tree mortality.
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Keywords: Mountain pine beetle; Ponderosa pine; *Dendroctonus ponderosae*; Bark beetles

1. Introduction

Periodic elevated populations of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, can cause significant mortality in ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., in the Black Hills of South Dakota and Wyoming. This tree mortality, although natural and caused by a native insect, can present challenges for managers and the public. Disruption of visual corridors devalues the recreational experience of visitors in areas where tourism is a major contributor to the local economy. Recreation sites, such as campgrounds and lake areas are also affected and require financial and human resources to remove hazard trees that may create unsafe conditions for visitors. Areas designated for timber production are also impacted, affecting forest planning processes and negating timber management investments. Moreover, high levels of tree mortality in stands managed for wildlife habitat, such as the northern goshawk, *Accipiter gentilis* (Linnaeus 1758) can compromise efforts.

Various studies have addressed different stand conditions and site characteristics associated with ponderosa pine susceptibility to mountain pine beetle (Fettig et al., 2007)

* Corresponding author. Tel.: +1 970 498 1252; fax: +1 970 498 1314.
E-mail address: jnegron@fs.fed.us (J.F. Negrón).

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but most have focused on even-aged managed stands. Sartwell (1971) indicated that slow growth and crown ratios $\leq$30% were associated with nearly all ponderosa pines killed by mountain pine beetle in the Pacific Northwest in second-growth even-aged stands. This author also reported increased mortality levels caused by mountain pine beetle with increasing stand density and suggested that tree competition, primarily for soil moisture, fosters an increased likelihood of mountain pine beetle attack.

In the Black Hills, Sartwell and Stevens (1975) examined 44 groups of mountain pine beetle infestation in second-growth even-aged ponderosa pine stands and found that stands with basal area >34.4 m^2/ha were more susceptible to mountain pine beetle. Schmid and Mata (1992) established long-term plots to determine the relationship between stand density and occurrence of mountain pine beetle in partially cut even-aged ponderosa pine stands. Their results suggested a critical threshold for susceptibility to mountain pine beetle at a basal area of 27.5 m^2/ha. Their later work (Schmid and Mata, 2005) indicated that perhaps the threshold for high susceptibility may be closer to 22.3 m^2/ha. Also in the Black Hills, Olsen et al. (1996) examined spatial variation in even-aged ponderosa pine stands in the Black Hills and concluded that stocking was higher in areas prone to mountain pine beetle infestation. The authors suggested that variation in stand conditions resulted in clusters of trees with different probabilities of infestation.

Most of the knowledge from uneven-aged ponderosa pine stands comes from the Colorado Front Range, the eastern slope of the continental divide in north-central Colorado. McCambridge et al. (1982) examined the characteristics of ponderosa pine stands infested by mountain pine beetle in north-central Colorado. Basal area prior to infestation was significantly higher in areas that experienced large amounts of tree mortality. Negrón and Popp (2004) also reported that stands infested by mountain pine beetle had significantly higher total basal area, ponderosa pine basal area, stem density, and stand density index. The authors developed several classification models for estimating the probability of infestation by mountain pine beetle based on stocking levels. Increased likelihood of attack was observed with a ponderosa pine basal area >17.1 m^2/ha.

Based on these studies and many others (see Fettig et al., 2007) it is clear that stand density plays a major role in determining stand susceptibility to mountain pine beetle. As land managers increase the application of uneven-aged management, information on stand and tree susceptibility to mountain pine beetle in these stands will be essential. It is important to examine uneven-aged ponderosa pine susceptibility to mountain pine beetle across the range of the species as differences in forest structure are common. Growing conditions for ponderosa pine are much more favorable in the Black Hills compared to the poor sites typical of the Colorado Front Range (Mogren, 1956; Schubert, 1974; Shepperd and Battaglia, 2002). Sartwell (1971) and Sartwell and Stevens (1975) indicated that poor sites experienced higher levels of mountain pine beetle-caused tree mortality than did high quality sites of similar initial stocking. Ponderosa pine forests in the Black Hills are denser (Shepperd and Battaglia, 2002) with a rather even distribution of trees and are intensively managed. This contrasts with Colorado Front Range forests that are characterized by a clumpy tree distribution mixed with meadows (Peet, 1981) and are scantly managed.

In this study, our objective is to examine stand and tree conditions in uneven-aged ponderosa pine forests in the Black Hills stands to identify characteristics that may be conducive to mountain pine beetle infestation. This knowledge will be of benefit in managing uneven-aged ponderosa pine stands by providing guidelines for minimizing mountain pine beetle-caused mortality.

2. Methods

2.1. Study site

The Black Hills are located in the western part of South Dakota and northeastern Wyoming. Ponderosa pine is the dominant forest tree across the Black Hills, with quaking aspen, *Populus tremuloides* Michx, white spruce, *Picea glauca* (Moench) Voss, and bur oak, *Quercus macrocarpa* Michx, present to a lesser degree. Elevation ranges from 1219 m east of the Hills to 2164 m in the west. Precipitation increases with northing and in higher elevations. Mean annual precipitation is about 41 cm in the southern Hills and 49 cm in the northern Hills with November through February being the driest months and May and June the wettest. Temperatures are also generally cooler in the northern Hills and higher elevations. Mean annual temperatures range from about 9 to 2.9 °C, mean annual highs from 17.9 to 11.4 °C, and mean annual low temperatures from 2.1 to −5.6 °C, from south to north, respectively. Soils are quite variable across the area and include 107 different series (Shepperd and Battaglia, 2002).

2.2. Plot establishment and data collection

The study was conducted during the summer of 2004. We used aerial detection flight data collected by the USDA Forest Service, Forest Health Management, to identify areas where mountain pine beetle-caused pine mortality was present. Using Black Hills National Forest vegetation data we overlaid a map portraying uneven-aged stands over the aerial survey data. We then randomly selected areas for sampling and plot establishment.

As uneven-aged stands have an irregular stocking distribution (Smith, 1986) we used a cluster sampling approach to minimize the influence of irregular stocking. We established a total of 84 clusters of four plots. Each cluster included one infested plot and three uninfested plots. Infested plots included at least one ponderosa pine killed by mountain pine beetle. Uninfested plots included at least one ponderosa pine $\geq$15.2 cm in diameter at breast height (1.4 m) (dbh hereafter) and no trees killed by mountain pine beetle. To determine plot center for infested plots, we would approach a group of trees killed by mountain pine beetle and identify trees that were initially killed by the insect within these groups. Trees initially killed were determined by foliage discoloration and the presence or absence of small branches. At this point, random numbers for distance and azimuth were obtained that would determine the precise location of plot center. Uninfested plots were located at azimuths of 75°, 195°, and 315° from the center of the infested plot and at a distance of 40.6 m. If infested trees were present where the uninfested plot was to be located we adjusted by increasing the distance by 20.3 m until a location for an uninfested plot was identified. Plots were circular and comprised an area of 0.02 ha.

For all plot trees ≥2.54 cm dbh, we recorded species, dbh, crown position, and tree status using the following categories: live, mountain pine beetle-killed, currently infested, pitchout (unsuccessful mountain pine beetle attack), or dead from other causes. Site information for plots included elevation, landform position, slope, and aspect.

2.3. Data analysis

We calculated mean dbh for all species combined and for ponderosa pine, total basal area, trees per hectare, and stand density index (SDI) for all species combined and for ponderosa pine for all plots. Stand density index values were obtained by summation of the individual tree utilization of the site (Stage, 1968; Long and Daniel, 1990). We also calculated the basal area per plot and mean tree diameter comprised of trees equal to or greater than 20.3, 25.4, 30.5, 35.6, and 40.6 cm.

To compare variables measured between infested and uninfested plots we first checked for normality by using the Shapiro–Wilk test. As most of the variables measured were not normally distributed for infested or uninfested plots we used the Wilcoxon rank-sum test to examine differences (Hollander and Wolfe, 1999).

To identify variables that may identify plots more likely to be attacked by mountain pine beetle we used classification trees. This approach identifies variables that can split the data into homogenous groups (Breiman et al., 1984). Linear regression and regression trees were used to model the extent of mortality in infested plots in terms of basal area killed using the variables measured as independent factors.

We then prepared graphs portraying the number of ponderosa pine trees per diameter class in uninfested and infested plots and compared their distributions using a Chi-square test. We also examined the number and percent of trees killed by mountain pine beetle across 5 cm diameter classes in the infested plots.

Probability of individual tree attack within infested plots was examined using logistic regression with a logit function (SAS Institute, 1999). Using the logistic approach, models take the form:

$$P(\text{infestation}) = \frac{1}{(1+\mathrm{e}^{-b'X})},$$

where $b'X$ represents a linear combination of explanatory variables X with their estimated parameters b, and e is the base of natural logarithms.

Predictor variables tested were plot measurements and tree diameter. Model performance was tested in a cross-validation framework. Observations were randomly divided into six groups with an equal number of infested trees assigned to each group. A model was parameterized using data from five of the six groups and its predictive value tested with the sixth group. The process was repeated five times so that every group was used for model construction and for model testing. We then examined model response across a range of diameter classes and stand density indices.

3. Results

Significant differences between infested and uninfested plots were observed for total basal area, ponderosa pine basal area, stand density index for all species and for ponderosa pine, for basal area in trees ≥25.4 cm dbh, percent basal area in ponderosa pine, and slope (Table 1). Infested plots had higher values than uninfested plots for all stocking variables and percent basal area in ponderosa pine. Although differences were detected for slope they are negligible and are of no biological importance.

Table 1
Mean (S.E.M.) stand conditions in uninfested *Pinus ponderosa* stands and those infested by *Dendroctonus ponderosae*, Black Hills NF, South Dakota and Wyoming, Summer 2004

Variable	Uninfested stands $N = 224$	Infested stands $N = 84$	P-value[a]
Trees per hectare – all species	582.8 (34.7)	629.9 (34.6)	.6978
DBH (cm) – all species	21.1 (0.7)	22.8 (0.9)	.2247
Total basal area (m^2/ha) – all species	22.0 (1.0)	26.3 (1.2)	.0157
Stand density index – all species[b]	415.1 (19.0)	495.0 (25.3)	.0269
Trees per hectare – ponderosa pine	503.0 (30.8)	555.2 (39.5)	.4876
DBH (cm) – ponderosa pine	22.1 (0.7)	23.3 (0.9)	.3739
Basal area (m^2/ha) – ponderosa pine	20.8 (1.0)	25.4 (1.2)	.0048
Stand density index – ponderosa pine	387.7 (17.8)	475.2 (24.7)	.0123
Percent basal area in ponderosa pine	95.0 (1.0)	97.0 (1.0)	.0004
Basal area (m^2/ha) in trees ≥25.4 cm	15.6 (0.9)	18.5 (1.0)	.0153
Elevation (m)	1814 (23)	1827 (22)	.7583
Slope	3.2 (0.2)	3.0 (0.3)	.0502

[a] Wilcoxon rank sum test.
[b] The stand density values in the table are calculated on a per hectare basis. For a per acre value: SDI acre = SDI hectare/2.47.

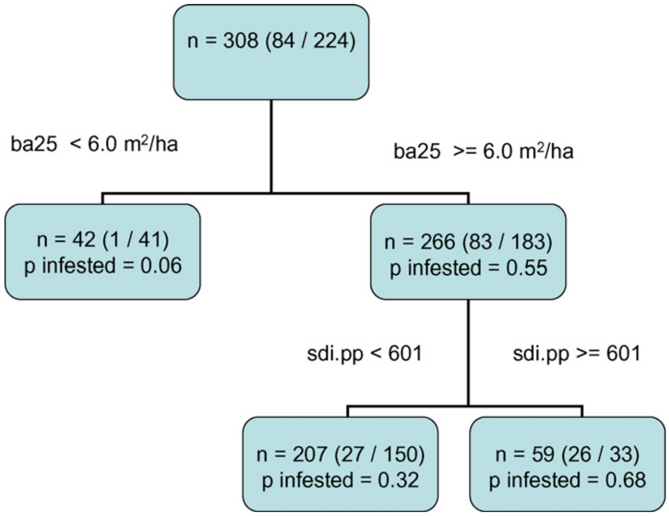

Fig. 1. Classification tree for discriminating between uninfested *Pinus ponderosa* plots and those infested by *Dendroctonus ponderosae*. ba25 is the basal (m^2/ha) comprised by trees ≥ 25.4 cm and sdi.pp is the stand density index including ponderosa pine only. Numbers in parenthesis indicate the number of infested and uninfested plots in each node. Probability infested = (number infested in node/number infested in root node)/(number infested in node/number infested in root node) + (number uninfested in node/number uninfested in root node), Black Hills NF, South Dakota and Wyoming, Summer 2004.

Classification tree analysis identified basal area comprised by trees equal to or greater than 25.4 cm dbh (ba25 hereafter) and ponderosa pine stand density index as useful variables for classifying infested and uninfested plots (Fig. 1). When ba25 is less than 6.0 m^2/ha the estimated probability of infestation was only 0.06. When ba25 is equal to or greater than 6.0 m^2/ha, the estimated probability of infestation was 0.55. When ba25 is equal to or greater than 6.0 m^2/ha, another split in the data using ponderosa pine stand density index can be used. When ponderosa pine stand density index is less than 601 the estimated probability of infestation was 0.32 and when ponderosa pine stand density index is equal to or greater than 601, then the estimated probability of infestation was 0.68.

A regression tree was constructed for estimating the average expected mortality on infested plots given an initial ponderosa pine basal area (Fig. 2). Splitting basal area levels were 38.1 and 27.8 m^2/ha. Expected mortality when ponderosa pine basal area is $\geqslant$38.1 m^2/ha is 19.3 m^2/ha. With ponderosa pine basal area <38.1 m^2/ha but $\geqslant$27.8 m^2/ha the expected mortality is 12.2 m^2/ha. When ponderosa pine basal area is <27.8 m^2/ha, then expected mortality is 7.4 m^2/ha. Linear regression also produced models to estimate the extent of observed mortality in the infested plots. Increasing ponderosa pine basal area or ponderosa pine stand density index resulted in increased estimated mortality (Fig. 3a and b).

Examination of the number of ponderosa pines across diameter classes portrays the similarity between infested and

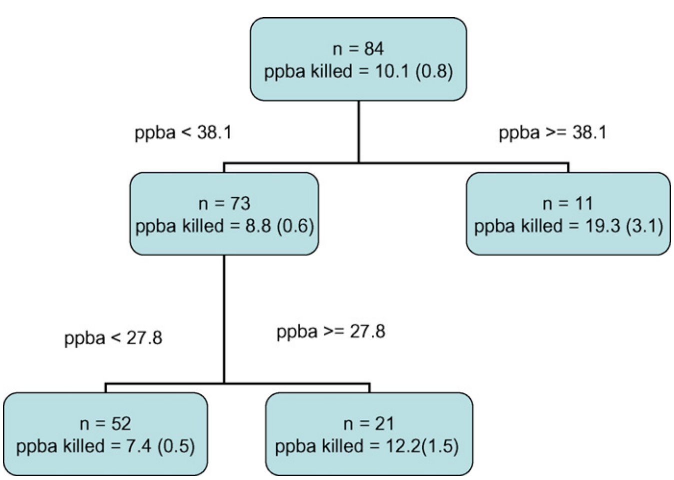

Fig. 2. Regression tree for estimating extent of mortality in *Pinus ponderosa* stands infested with *Dendroctonus ponderosae*. ppba is the basal area (m^2/ha) comprised by ponderosa pine only. Numbers in parenthesis inside boxes indicate the standard error of the mean, Black Hills NF, South Dakota and Wyoming, Summer 2004.

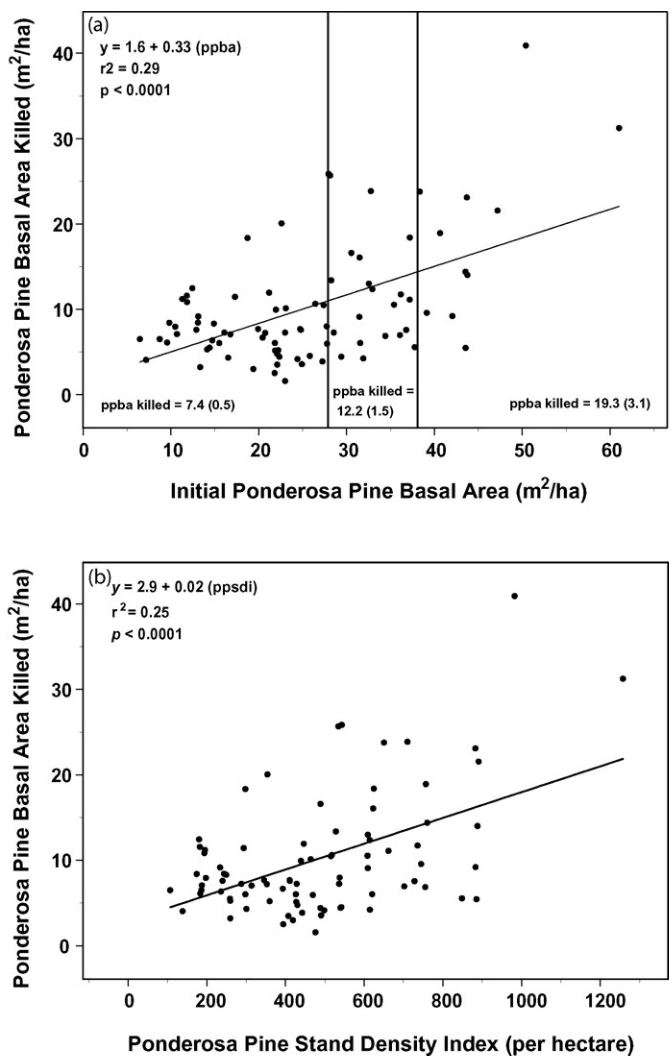

Fig. 3. Linear regression for describing the relationship between initial *Pinus ponderosa* basal area (ppba) (a) or *Pinus ponderosa* stand density index (ppsdi) (per hectare) (b) and *Pinus ponderosa* basal area killed by *Dendroctonus ponderosae*. Numbers in parenthesis indicate the standard error of the mean, Black Hills NF, South Dakota and Wyoming, Summer 2004.

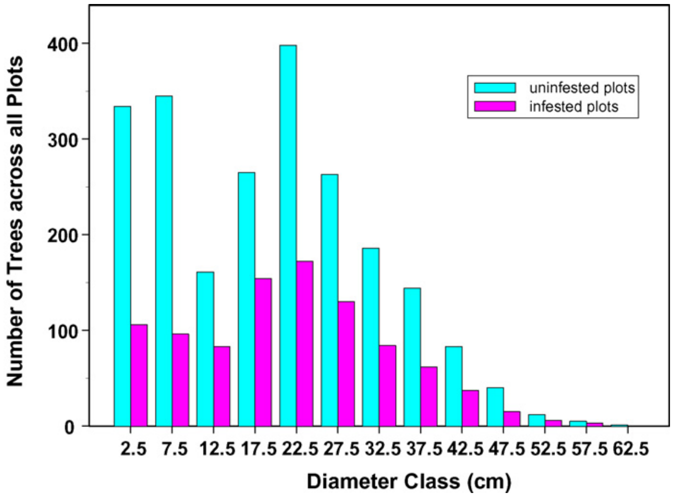

Fig. 4. Number of *Pinus ponderosa* per diameter classes across all uninfested and infested plots, Black Hills NF, South Dakota and Wyoming, Summer 2004.

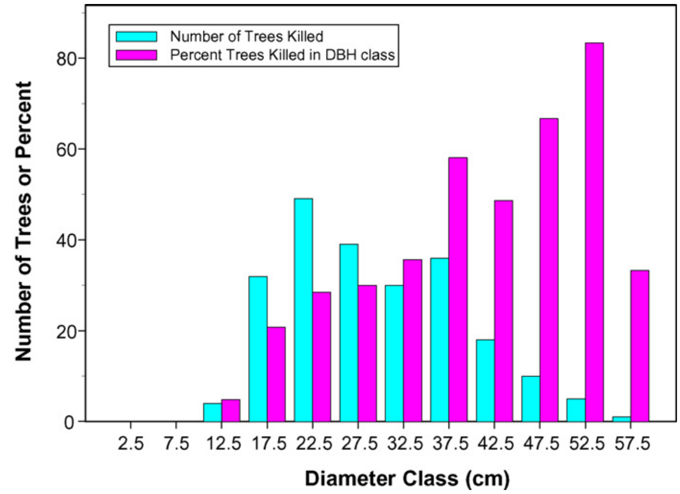

Fig. 5. Number and percent of *Pinus ponderosa*, trees killed by *Dendroctonus ponderosae* by diameter classes, Black Hills NF, South Dakota and Wyoming, Summer 2004.

uninfested plots (Fig. 4). Although the distributions were statistically different from one another (Chi-square = 49.6, df = 12, $P < 0.01$), this was likely the result of a deficit in uninfested plots in the 12.5 cm class which is larger than the deficit observed in infested plots as these relate to the rest of the size classes. In both cases the largest number of trees was in the 22.5 cm class. The differences in the number of trees observed, being higher numbers in the uninfested plots, only reflects that more uninfested plots were sampled in the study. Most of the mountain pine beetle-killed trees in the infested plots were in the 17.5–37.5 cm classes (Fig. 5). The percent of trees killed by diameter classes increased with diameter class with the exception of the 42.5 cm class; there were only 6 and 3 trees in the 52.5 and 57.5 cm diameter classes, respectively. No trees were killed by mountain pine beetle in the two smallest diameter classes (Fig. 5).

Logistic regression modeling for estimating the probability of attack on an individual tree in infested plots produced two models (Table 2). A one-variable model indicated that the estimated probability of attack increased with tree diameter. A two-variable model indicated that in addition to increasing tree diameter, increased ponderosa pine stand density index was associated with increased estimated probability of attack. Cross-validation analysis indicated estimated correct classification ranging from 65 to 73%. Correct classifications were higher for infested trees, ranging from 62 to 89% (Table 3).

Table 2
Logistic model parameters for estimating probability of individual *Pinus ponderosa* tree attack by *Dendroctonus ponderosae* within infested plots, Black Hills NF, South Dakota and Wyoming, Summer 2004

Model	Variable	Estimate	S.E.	*P*-value
1 variable	Intercept	−3.5	0.3	<0.0001
	Tree DBH	0.3	0.02	<0.0001
2 variable	Intercept	−4.2	0.4	<0.0001
	Tree DBH	0.3	0.02	<0.0001
	Ponderosa pine stand density index	0.003	0.001	0.0487

Model performance for the one-variable model using tree diameter and the two-variable model using tree diameter and ponderosa pine stand density index is presented in Fig. 6a and b. The estimated probability of attack attains 0.92 when dbh is 61 cm, the largest tree size observed in our study. When ponderosa pine stand density is included then the estimated probability of individual tree infestation for a 61 cm dbh tree is 0.9 at a ponderosa pine stand density index of 250 and 0.96 with a ponderosa pine stand density index of 1250.

4. Discussion

Our classification tree model identified higher basal area in trees ≥25.4 cm dbh and ponderosa pine stand density index as being correlated with a higher estimated probability of plot infestation. This is similar to the findings of Negrón and Popp (2004) in the Colorado Front Range where total basal area and ponderosa pine basal area were associated with the probability of infestation. Our data indicates however, that in the Black Hills it is the basal area comprised by mid- to large-size that make a stand more susceptible. This contrasts with even-aged stands where it is the total contribution of ponderosa pine that is a factor in stand susceptibility.

Table 3
Results of cross-validation analysis for a model estimating the probability of individual *Pinus ponderosa* tree infestation by *Dendroctonus ponderosae* within infested plots using tree diameter and ponderosa pine stand density index, Black Hills NF, South Dakota and Wyoming, Summer 2004

Group	Overall correct classification	Uninfested trees correct classification	Infested trees correct classification
1	0.67	0.58	0.76
2	0.65	0.62	0.67
3	0.65	0.68	0.62
4	0.73	0.61	0.86
5	0.73	0.58	0.89
6	0.72	0.59	0.84

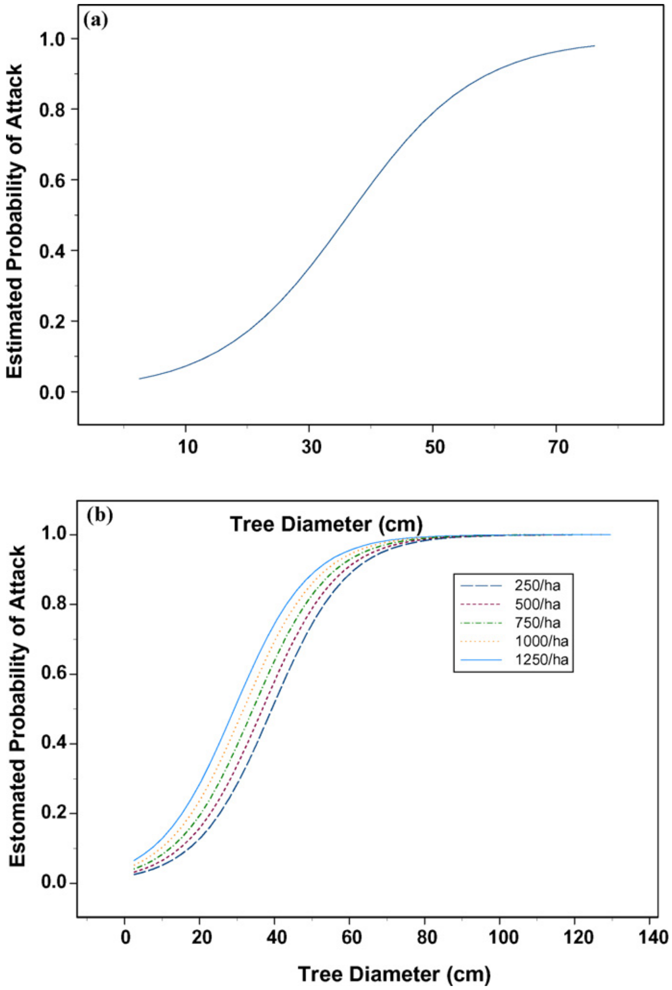

Fig. 6. Probability of *Pinus ponderosa* individual tree infestation by *Dendroctonus ponderosae* within infested plots as influenced by (a) tree diameter and (b) by the combination of tree diameter and *Pinus ponderosa* stand density index, Black Hills NF, South Dakota and Wyoming, Summer 2004.

Regression trees and linear regression modeled increased mortality levels with increasing stocking levels. Although the R^2 in the linear relationships are modest, the relationship is consistent with many other studies. The split at 27.8 m^2/ha identified in the regression tree is consistent with studies conducted by Schmid and Mata (1992) that suggested that this may be the threshold for high susceptibility in even-aged stands. Although Schmid and Mata (2005) later suggested that the threshold may be more around 23 m^2/ha. Results from the regression tree divide the data in what can be considered low, medium, and high potential tree mortality classes. These are represented by the reference lines over the linear regression using initial basal area (Fig. 3a). It should be noted that these damage classes are derived from empirical data and are not arbitrary levels as the regression tree groups these into classes with the least variance. These classes should prove useful for managers in identifying potential mortality levels in uneven-aged ponderosa pine stands.

Previous studies have indicated that given the presence of suitable diameter classes, increased basal area is associated with increased likelihood and increased levels of bark beetle-caused tree mortality (see Fettig et al., 2007). McCambridge et al. (1982) indicated increased mountain pine beetle-caused mortality in ponderosa pine in Colorado in areas of higher basal area and higher trees per hectare when compared to areas of less stocking. Sartwell and Stevens (1975) reported higher ponderosa pine mortality levels caused by mountain pine beetle in the Black Hills of South Dakota and suggested 34.4 m^2/ha as a threshold beyond which stands are more likely to become infested. Also working in the Black Hills, Schmid and Mata (1994) lowered the threshold in even-aged stands to growing stocking level (GSL) of 120 (GSL = basal area when average stand diameter is 25.4 cm so GSL 120 $\approx$ 27.5 m^2/ha). Schmid and Mata (2005) further suggest that the threshold may be closer to GSL 100 ($\approx$ 23.0 m^2/ha). In southwestern ponderosa pine, roundheaded pine beetle, *Dendrocotnus adjunctus* Blandford, caused tree mortality is correlated with increasing basal area and associated reduced growth rates (Negrón, 1997; Negrón et al., 2000).

Studies in other forest types and associated bark beetles have also reported similar results. Some include lodgepole pine, *Pinus contorta* Dougl. ex. Loud.; white spruce, *Picea glauca* (Moench) Voss; Sitka spruce, *Picea sitchensis* (Bong.) Carr.; Lutz spruce, *Picea X lutzii* Little; Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco; and whitebark pine, *Pinus albicaulis* Engelm. (Amman et al., 1977; Amman et al., 1988; Amman and Logan, 1998; Holsten, 1984; Reynolds and Holsten, 1994, 1996; Furniss et al., 1979; Furniss et al., 1981; Negrón et al., 1999; Perkins and Roberts, 2003). Stand density index has also been used to estimate lodgepole pine stand susceptibility to mountain pine beetle (Anhold and Jenkins, 1987) and stand density diagrams have been proposed for managing lodgepole pine stands (Anhold et al., 1996). Stand density index was also a good predictor of piñon pine, *Pinus edulis* Engelm., mortality caused by the piñon ips, *Ips confusus* (LeConte) (Negrón and Wilson, 2003). For an extensive review on the relationship between stand conditions and bark beetle-caused mortality, and explanations of causal mechanisms the reader is referred to Fettig et al. (2007).

Examination of the size of trees killed by mountain pine beetle indicates that more trees were killed in the mid-size diameter classes although a higher percentage of the larger trees were killed. This is consistent with the identification of ba25 as a discriminating variable in the classification tree analysis. Negrón and Popp (2004) in the Colorado Front Range also reported a higher percentage of trees killed in the larger diameter classes. This is consistent with data presented by Schmid and Mata (2005) for even-aged stands. Also from the Colorado Front Range, McCambridge et al. (1982) observed increased number of ponderosa pines killed by mountain pine beetle as dbh increased to 22.9 cm, about the same percent of trees killed in diameter classes between 20.3 and 35.6 cm and no trend with trees larger than 35.6 cm, although the sample size in this class was small.

Our logistic regression modeling of the probability of individual tree infestation in infested plots indicated a higher estimated probability of attack with increasing tree diameter. The model using tree diameter and ponderosa pine stand density index indicated that the probability of individual tree attack is modified by stand density. The estimated probability of individual tree attack surpassed 0.5 with a tree diameter from 30.5 cm at the higher stand density index evaluated to 40.6 cm at the lowest. Under higher stand density an estimated probability of attack approached 1 with a smaller diameter tree. Trees in the same diameter class have a higher likelihood of being attacked in a denser stand. To our knowledge, this is the first quantitative description of this interaction between tree diameter, stand density, and individual tree susceptibility. This suggests that when describing tree diameter preferences for bark beetles stocking levels need to be considered.

Studies in lodgepole pine indicate that mountain pine beetle preferentially selects the larger trees in a stand (Cole and Amman, 1969; Mitchell and Preisler, 1991). Olsen et al. (1996) indicated that mountain pine beetle did not exhibit preference for larger trees in an even-aged Black Hills ponderosa pine stand. In our study, it is not known if larger diameter trees were first attacked, but over the course of the outbreak a higher percentage of the larger trees were killed.

Reduced susceptibility with lower stocking has been attributed to be a result of increased vigor (Larsson et al., 1983) and subsequent effect on tree resistance (Kolb et al., 1998). Alternatively, it has been suggested to be as a result of different stand microclimates with more open stands being less conducive to beetle populations (Bartos and Amman, 1989; Amman and Logan, 1998). More than likely a combination of these factors is important in determining why bark beetles attack more frequently and cause more mortality in high density stands.

Uneven-aged management in the Black Hills is used to create more open and diverse forests with high structural and spatial diversity which would be less susceptible to stand replacement fire (Agee and Skinner, 2005) or insect outbreaks (Fettig et al., 2007). This can be accomplished with moderate stocking of small diameter trees and retention of larger diameter trees with a basal area of 13.7 m^2/ha or less (Shepperd and Battaglia, 2002). This basal area level is below what has been suggested as a threshold for low susceptibility to mountain pine beetle in even-aged stands (Schmid and Mata, 2005). It is also below the level reported to increase the probability of infestation in uneven-aged ponderosa pine in the Colorado Front Range (Negrón and Popp, 2004). The Colorado Front Range growing sites are poor (Mogren, 1956; Schubert, 1974), particularly when compared to the Black Hills (Shepperd and Battaglia, 2002). This agrees with the work of Sartwell and Stevens (1975) who suggested that better sites can carry higher basal area levels while maintaining lower susceptibility to mountain pine beetle. Sartwell (1971) also observed higher mortality levels in poor sites.

From a managerial perspective use of the first split, ba25, in the classification tree for the estimated probability of attack should suffice. Inclusion of the second split, stand density index, can further refine the ability to identify susceptible stands as the estimated probability of attack doubles when ponderosa pine stand density index is greater or equal to 601.

In summary, plots infested by mountain pine beetle exhibited a higher stocking level which is also the case in even-aged stands. Stocking levels play a major factor in influencing mountain pine beetle susceptibility in uneven-aged stands much like it does in even-aged stands. However, in uneven-aged stands it is the presence of mid- to large-diameter classes that plays a major role. The estimated probability of individual tree attack increased with tree diameter in the infested plots, but it was also influenced by stand density. A tree of a given diameter size is more likely to be infested in a denser stand. In plots with of similar stand density, those with a higher basal area in trees in mid to large size classes, as compared to those with a higher proportion in small dbh trees, are more susceptible to mountain pine beetle attack. If retention of larger diameter trees is a management objective, regulating stocking levels with particular attention to the basal area in trees larger than 25 cm dbh will be of benefit.

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